

UBLS-82-1

BENTHIC INVERTEBRATE COMMUNITIES
IN THE FLUCTUATING RIVERINE HABITAT
BELOW CONOWINGO DAM

Prepared By

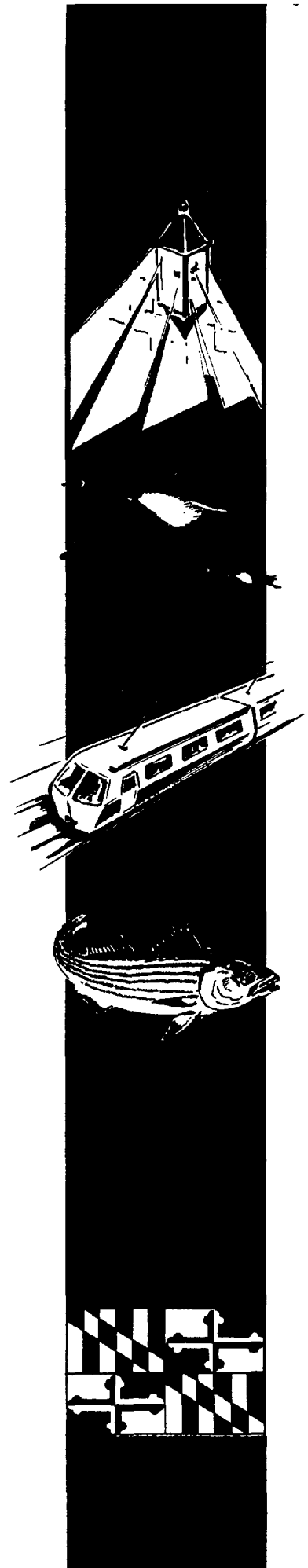
Environmental Center
Martin Marietta Corporation
1450 South Rolling Road
Baltimore, Maryland 21227

March 1982

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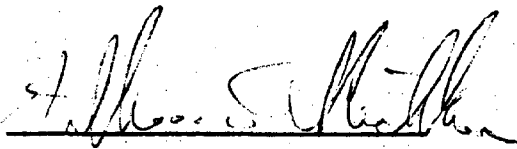
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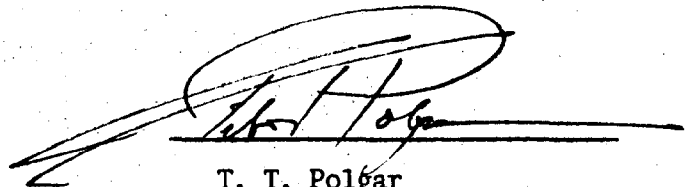
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FOREWORD

This report summarizes the findings of a benthic invertebrate study conducted on the Susquehanna River in the vicinity of the Conowingo Dam and hydroelectric generating station. The field work was performed by NTSC Technical Services, McLean, VA, for the Power Plant Siting Program (PPSP) of the Maryland Department of Natural Resources from June through November 1980 under PPSP contract P16-80-05. Data analyses and report preparation were carried out by the Martin Marietta Environmental Center in 1981 under contract P16-82-03.

ABSTRACT

Variations in the release of water from hydroelectric projects can strongly affect the availability of suitable habitats for downstream benthic invertebrates. To examine the extent of this problem in the Susquehanna River below Conowingo reservoir, basket samples were deployed by NTSC Technical Services, Inc., along four transects in three habitats: constantly submerged channels, pools that become isolated at low flow, and areas exposed at low flow. Samplers were incubated for 3-week periods from June through October. Data collected were analyzed by the Martin Marietta Environmental Center. Exposed habitats contained significantly fewer organisms than either of the other habitats along all four transects. Differences in the benthic communities between channel and isolated pool habitats were greatest at the transect nearest the dam. Gammarids and dipterans were most abundant in channel habitats while molluscs dominated in the isolated pools. Variation in dam-regulated river flow and the resulting difference in food input from the reservoir are apparently important determinants of the benthic invertebrate community structure below the dam.

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I. INTRODUCTION

Water flow in the lower reaches of the Susquehanna River is substantially influenced by the Conowingo Dam and its associated hydroelectric generating station. The effects are large because the generating station operates as a peaking power unit; that is, water is collected and stored within the reservoir during most of the day until power is needed to supplement the more continuous generating stations (i.e., fossil fuel or nuclear plants). This type of peaking results in large volumes of water released through the turbines, exacerbating the already large seasonal variability in normal river discharge, and is viewed as detrimental to the riverine biota located downstream of peaking hydroelectric projects (Stanford and Ward, 1979).

Previous studies have indicated that both the abundance and composition of zoobenthic communities are altered by the fluctuations of discharge from hydroelectric projects. Fisher and LaVoy (1972) concluded that water level fluctuations due to peaking power generation might prevent the establishment of normal benthic invertebrate communities in areas that were periodically exposed. The most notable result of their studies on the Connecticut River is the observed shift from mollusc predominance in areas least often exposed to dominance by chironomids and oligochaetes in those most often exposed. Benthic invertebrates that require relatively high current velocities were absent or nearly so in a run of river below a hydroelectric project in Maine (Trotzky and Gregory, 1974). Henricson and Müller (1979) pointed out four factors that account for the effects of regulated discharge on zoobenthic communities: 1) short-term regulation, 2) altered temperatures, 3) poor plankton drift, and 4) increased sediment transport.

RATIONALE AND OBJECTIVES

It was hypothesized earlier that the mode of operations at the Conowingo Dam generating station could reduce zoobenthic biomass in areas that were exposed during shutdown periods (Polgar and Dwyer, 1979). The result would be reduced food availability for some resident and anadromous fishes in the area downstream of the dam. The station shutdowns occur at night and during a

majority of the time on weekends. Reduced discharge during these shutdown periods drastically alters the benthic habitats below the dam.

The objective of the present study was to examine the effects of the variation of discharge from Conowingo Dam on the benthic invertebrate community downstream of the dam. Specifically, the availability and utilization of three habitat types by benthic invertebrates were investigated. i.e.,

- Channel - habitats constantly submerged and through which water always flows regardless of dam discharge
- Isolated pools - areas into and out of which no water flows at low dam discharges
- Exposed - areas dewatered at low dam discharges.

II. METHODS

All field and laboratory work was carried out by NTSC under the direction of Mr. Barry Nichols. Benthic invertebrate samples were collected from three habitat types located on each of four transects on the Susquehanna River downstream of Conowingo Dam (Fig. II-1). The four transects correspond to those established earlier by the Susquehanna River Basin Commission (Jackson and Lazorchick, 1978).

Benthic organisms were collected in barbeque baskets (16 cm in diameter, 25 cm long) filled with 2-in. to 3-in. diameter rocks which had been cleaned of all organisms. Each basket was moored in the appropriate habitat with 4-meter lines attached to eyebolts imbedded in the river substrate.

Table II-1 sets out the sampling periods and the number of replicate samplers incubated in the river during each period. Both 3-week and 6-week incubation periods were used during the study. However, due to the greater relative comprehensiveness of the 3-week incubation data, only those data are reported on here.

For retrieval, each sampler was placed in a plastic bucket while still submerged, and the bucket and basket were lifted out of the river. Each rock was then thoroughly scrubbed clean within the bucket. The bucket contents were sieved through a No. 30 (0.5-mm mesh) sieve, and the resulting concentrated sample was preserved in 10% formalin.

The benthic invertebrates were sorted and identified in the laboratory. Most identification was to the generic level. Dipteran larvae and nematodes were identified by Dr. William Banta of American University.

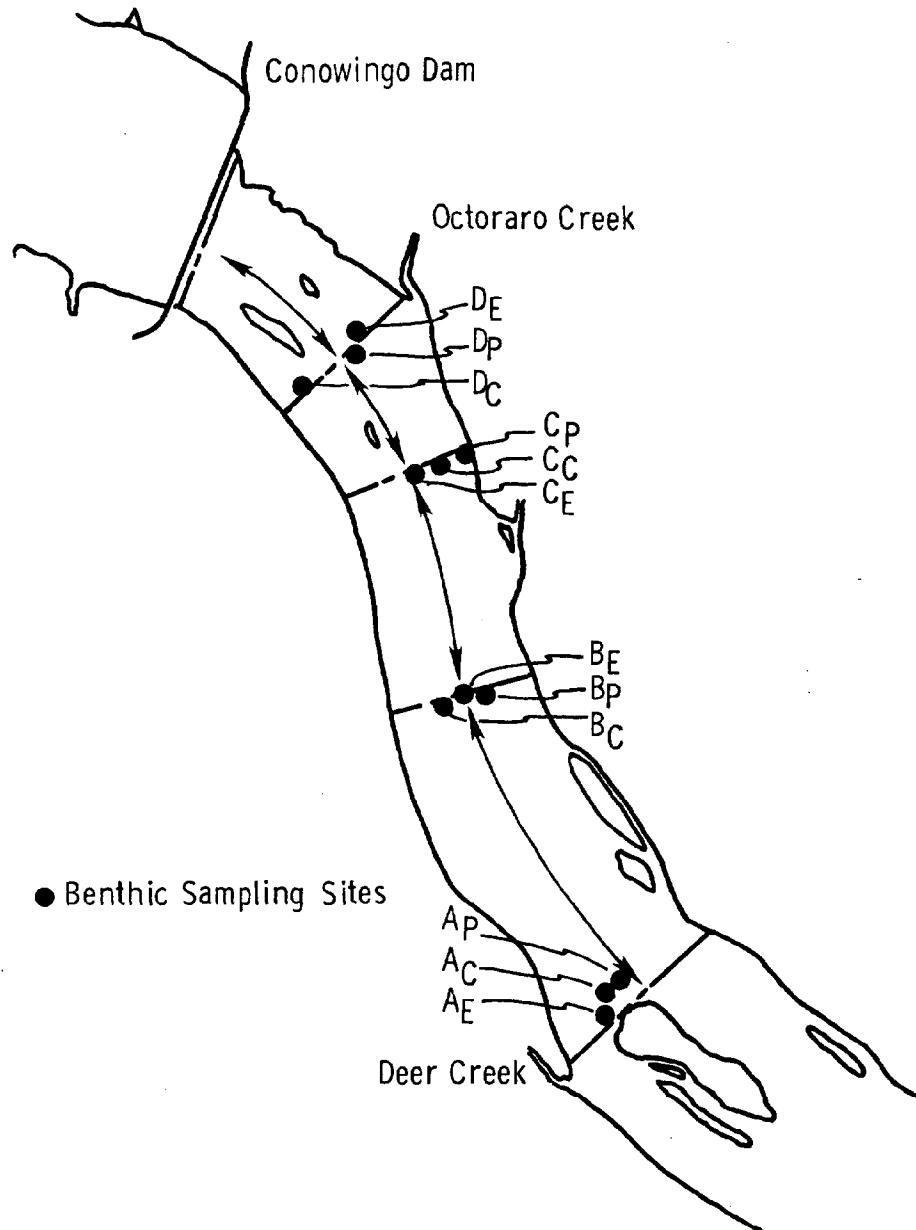


Fig. II-1. Map of Susquehanna River below Conowingo Dam indicating location of sampling sites. First letter signifies transect; subscripts signify habitat type: C = channel, P = isolated pool, E = exposed

Table II-1. Sampling periods and number of replicate samples retrieved during each period from the three habitats on each transect. * = no sample.

Sampling Period	Transect	A			B			C			D		
	Habitat ^(a)	C	E	IP	C	E	IP	C	E	IP	C	E	IP
1 June - 20 June		1	1	1	1	1	1	1	1	1	1	1	*
20 June - 13 July		1	*	1	1	1	1	1	1	1	1	1	*
13 July - 2 August		3	*	3	3	3	3	3	3	3	3	3	4
2 August - 24 August		4	2	4	4	4	4	4	4	4	4	4	4
24 August - 14 September		5	*	5	6	*	6	6	*	5	6	*	6
14 September - 4 October		5	*	5	6	*	6	6	*	6	6	*	6

(a) Habitat types: C = channel, E = exposed, IP = isolated pool.

III. STATISTICAL ANALYSIS

A total of 110 taxa were collected during the study period, although many were taken infrequently. The fifteen most abundant species, which cumulatively constituted 90% of the total abundance of organisms collected during the study, were used in the analyses described here.

For each of the most abundant species, the hypotheses of no differences in abundance among sampling dates, among transects, and among habitats were tested using a three-way analysis of variance (ANOVA). The underlying model in this analysis was:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik} + (\beta\gamma)_{jk} + (\alpha\beta\gamma)_{ijk} + \epsilon_{ijkl}$$

where

Y_{ijkl} = the l^{th} species abundance observed at the k^{th} habitat on the j^{th} transect on the i^{th} sampling date,

μ = the population mean,

α_i = the effect due to the i^{th} sampling date,

β_j = the effect due to the j^{th} transect,

γ_k = the effect due to the k^{th} habitat,

$(\alpha\beta)_{ij}$ = the interaction (combined effect) of the i^{th} sampling date and the j^{th} transect,

$(\alpha\gamma)_{ik}$ = the interaction of the i^{th} sampling date and the k^{th} habitat,

$(\beta\gamma)_{jk}$ = the interaction of the j^{th} transect and the k^{th} habitat,

$(\alpha\beta\gamma)_{ijk}$ = the interaction of the i^{th} sampling date, the j^{th} transect, and the k^{th} habitat, and

ϵ_{ijkl} = the experimental error associated with the l^{th} abundance observed on the i^{th} sampling date at the k^{th} habitat on the j^{th} transect.

The distribution of the error terms was assumed to be the same for all observations and normally distributed with a mean of 0 and a variance of σ^2 [$\epsilon_{ijkl} \sim N(0, \sigma^2)$]. Simply stated, the ANOVA model assumes equal variances

among the populations in the date-transect-habitat cells. This assumption of homogeneity of variances can be tested using Cochran's C statistic (Dixon and Massey, Jr., 1969), where $C = (s_{\max}^2 / \Sigma s^2)$. C was calculated for each species using raw data, $\log(X + 1)$ transformations, and square root transformations of the raw data. For most species, the hypothesis of equal variances was rejected with the raw data and square root-transformed data. Therefore, logarithmic-transformed data were used for all ANOVAs.

Differences in community structure among habitats were also of major interest. To examine these differences, multivariate analytical methods were deemed appropriate (Pielou, 1977). These methods not only take into account the variances of the individual species, but their covariances as well; thus, more information can be incorporated into the analyses than through a series of univariate ANOVAs for individual species. Specifically, a step-wise discriminant analysis was used to test the hypothesis of no differences among groups in the benthic communities. Groups were each identified by a particular transect and habitat. The analysis determined linear combinations of those species that contributed most to the discrimination of these groups. The coefficients of the linear combinations for the species variables were computed to achieve a maximum for the ratio of the variance among groups to the variance within groups. The species were chosen in a step-wise manner until no further significant additions to the discrimination of the groups could be made (Dixon, 1975). Species whose observation vectors were linear combinations of species previously entered were excluded in the analysis. Wilk's Lambda was used to test the significance of the among-groups difference in benthic communities.

Flow data for the Susquehanna River at Conowingo Dam were obtained from the United States Geological Survey. These data consisted of flow measurements in cubic feet per second (cfs) at 15-minute intervals. The mean and the variance of the flow for each of the six sampling periods were computed. The fraction of each sampling period during which the dam turbines were not operating was also calculated, using $63.7 \text{ m}^3/\text{s}$ as the benchmark flow. That is, any flow measurement less than $63.7 \text{ m}^3/\text{s}$ was assumed to indicate that the turbines were not operating. These periods also defined the fraction of time during which pool habitats were isolated and exposed habitats were dewatered.

The number of times in a sampling period the flow increased from values $< 63.7 \text{ m}^3/\text{s}$ to values $> 63.7 \text{ m}^3/\text{s}$, and vice versa, was assumed to indicate how often the turbines were turned on and off, respectively, i.e., variability in the turbine operations.

The variation in the presence of the isolated pool and exposed habitats was also assessed in this way. These results were used to relate differences in abundances observed among sampling periods, transects, and habitats to river flow and dam operations.

The most notable effect of low flows was the many areas that were exposed and, secondarily, the large number of pools that became isolated. Infrared aerial photographs indicated that 15-25% of the river bottom (at high flow) was exposed at a discharge of $\sim 56 \text{ m}^3/\text{s}$ (2000 cfs) (Photo Science, Inc., 1980). No estimation of the area comprising isolated pools has been made, but visual observation suggests that this area greatly exceeds the channel areas at low flows, near Transect D (R. Dwyer, pers. comm.).

IV. RESULTS

Table IV-1 presents the total number of benthic invertebrates collected from the three habitat types during the first four sampling periods. It is readily apparent that far fewer organisms were collected in baskets which were intermittently exposed than in the other habitats. Because of this obvious difference, no further samples were taken from the exposed habitats for the the two remaining periods of the study, and additional effort was spent in sampling the channel and pool habitats. All further analyses, therefore, refer only to data from these two habitats.

It can also be seen in Table IV-1 that the mean number of benthic invertebrates in the channel and isolated pool habitats was quite similar during the first four sampling periods. Figure IV-1 presents the mean number of organisms found in the channel and isolated pool habitats on each sampling date. Benthic invertebrate abundance in these two habitats at Transects B and D remained similar for most of the study period. There were, however, some marked differences among habitats at Transect C on the initial and final sampling dates and at Transect A over the last three sampling periods. The results of two-way ANOVAs computed for each transect confirm these findings (Table IV-2). Only at Transects A and C were differences between abundances in channel and pool habitats significant, and in both cases, the mean total number of invertebrates was significantly greater in the isolated pools.

Possible differences in community structure were also investigated. Table IV-3 presents those taxa which accounted for >90% of the organisms collected during the study. Of these 15 taxa, six were dipterans and three were gastropods. Gammarus lacustris, a ubiquitous amphipod, and the turbellarian, Dugesia tigrina, together accounted for >50% of the lower Susquehanna River benthic community.

The abundance of G. lacustris was variable throughout most of the study (Fig. IV-2). At Transects A and C, the number of G. lacustris collected from isolated pools consistently exceeded that from the channel habitat. However, at Transect B, with the exception of the first sampling period, there was little difference between the number of G. lacustris from the two habitats.

Table IV-1. Mean number of organisms per basket collected in each habitat on each transect in lower Susquehanna River during the first four sampling periods.

<u>TRANSECT</u>	<u>HABITAT</u>	<u>NUMBER/BASKET</u>
A	Channel	347
	Isolated Pool	572
	Exposed	3
B	Channel	492
	Isolated Pool	433
	Exposed	59
C	Channel	311
	Isolated Pool	577
	Exposed	27
D	Channel	800
	Isolated Pool	911
	Exposed	14

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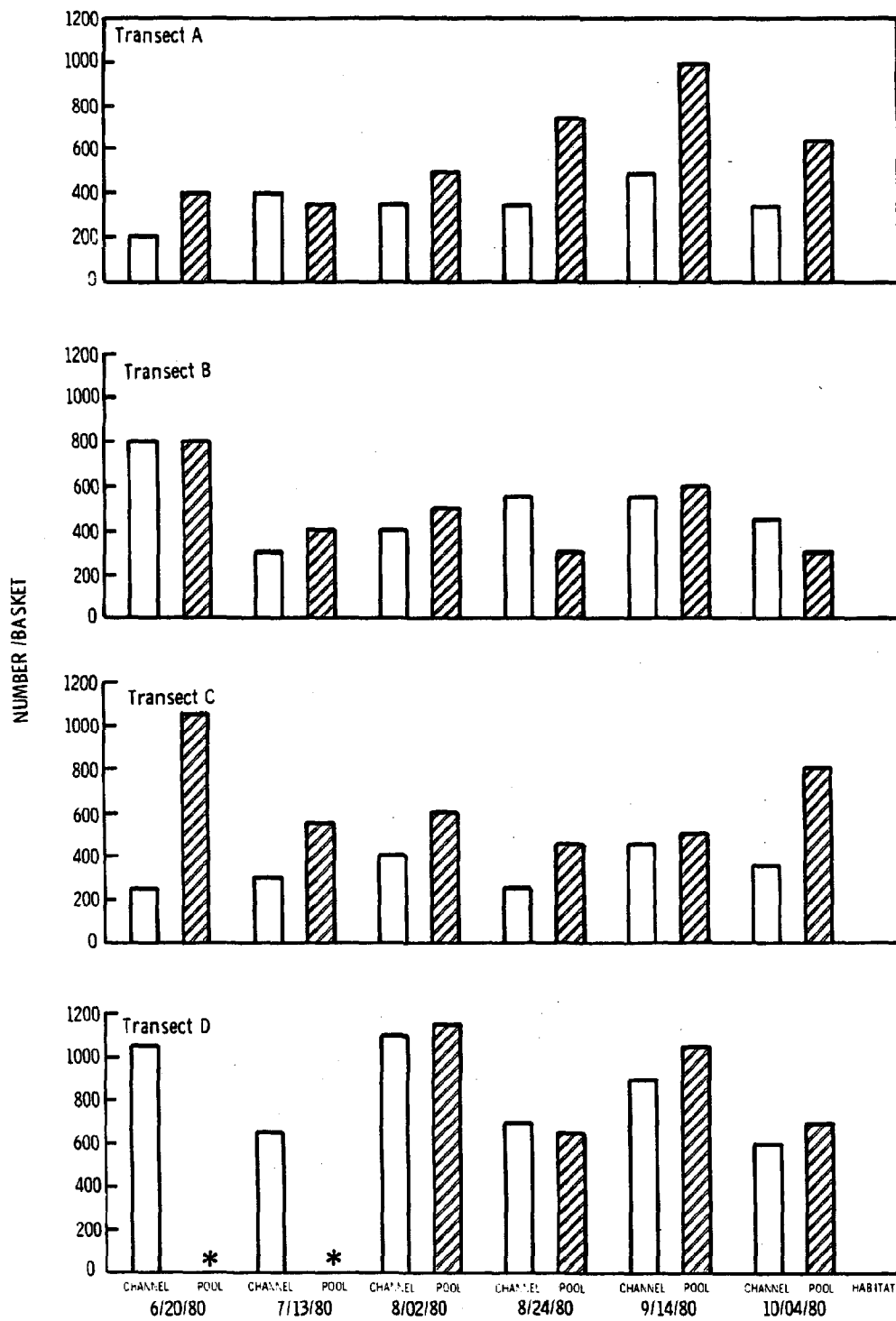


Fig. IV-1. Mean total number of benthic organisms observed in channel and isolated pool habitats on each transect during the six 3- week sampling periods. * = No sample

Table IV-2. Results of two-way ANOVAs, computed for each transect in lower Susquehanna River, comparing total benthic invertebrate densities with date and habitat as main effects. Only data for channel and isolated pool habitats are included.

<u>TRANSECT</u>	<u>EFFECT</u>	<u>p>F</u>
A	Habitat	0.011
	Date	0.0085
	Date * Habitat	0.5820
B	Habitat	0.4085
	Date	0.0007
	Date * Habitat	0.0207
C	Habitat	0.0001
	Date	0.1276
	Date * Habitat	0.0362
D	Habitat	0.4956
	Date	0.0933
	Date * Habitat	0.9623

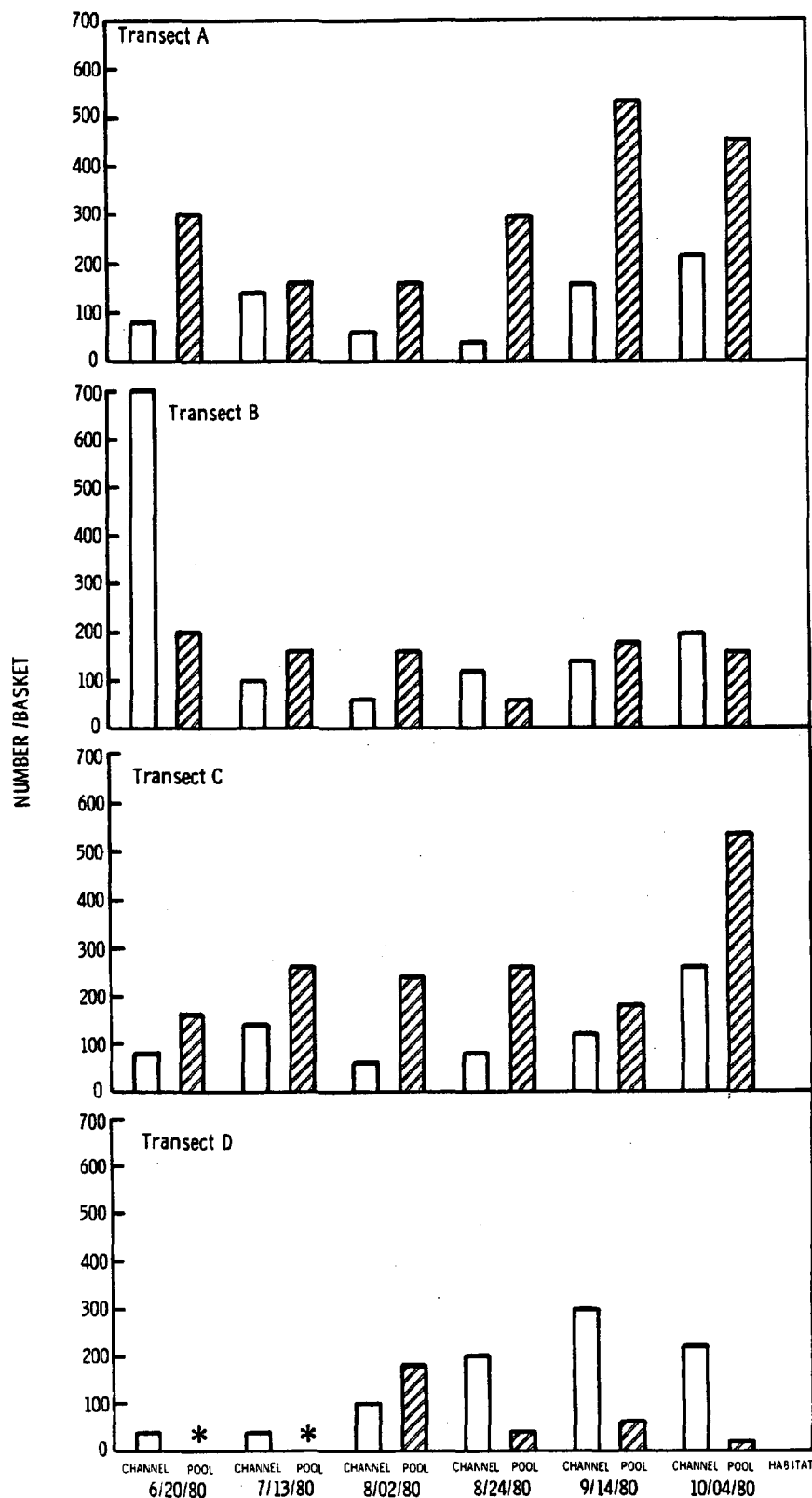


Fig. IV-2. Mean number of *Gammarus lacustris* observed in the channel and isolated pool habitats on each transect during the six 3- week sampling periods. * = No sample

Table IV-3. Taxa composing > 90% of the benthic community of the lower Susquehanna River below Conowingo Dam, June - October 1980.

<u>TAXON</u>	<u>PERCENT CONTRIBUTION</u>
<u>Gammarus lacustris</u>	32.2
<u>Dugesia tigrina</u>	25.1
<u>Dicrotendipes</u> sp.	5.5
<u>Cheumatopsyche</u> sp.	3.5
<u>Nais pseudobtusa</u>	3.5
<u>Gyraulis</u> sp.	3.5
<u>Cricotopus</u> sp.	3.3
<u>Tanytarsus</u> spp.	3.1
<u>Nais</u> sp.	2.1
<u>Hydra americana</u>	1.6
<u>Polypedilum</u> sp.	1.6
Chironomid pupae	1.3
<u>Ferrissia</u> sp.	1.3
<u>Glyptotendipes</u> sp.	1.3
<u>Ferrissia</u> sp.	1.2

At Transect D, G. lacustris was nearly totally restricted to channel habitats, especially during the last three sampling periods.

Dugesia tigrina was generally less abundant at Transects A, B, and C than at Transect D, where it was most numerous in the isolated pools (Fig. IV-3). At Transects A and C, isolated pools contained more D. tigrina; however, at Transect B, channel densities were greater. There was a marked seasonality in the density of D. tigrina at all transects, i.e., densities increased from June through July to a maximum in late August and early September.

The greatest among-transect differences in abundance of the 15 most abundant taxa were found for Tanytarsus sp. and Gyraulis sp. The density of the former was by far greatest at Transect D, and much lower at the downstream transects (Fig. IV-4). The opposite relationship applied for Gyraulis, which attained maximal densities at Transect A (Fig. IV-5). This gastropod was commonly found in both habitats at all transects, except Transect D where the greatest abundance was in isolated pools.

The statistical significance of the above differences was tested using a three-way ANOVA model with habitats, transects, and dates as main effects. The results of these analyses for each of the 15 most abundant taxa indicated numerous significant interactions of the three main effects (Table IV-4), which precluded meaningful interpretation of the significance of the main effects. Therefore, an alternative analytical approach was applied to determine significant among-habitat differences in the benthic invertebrate community structure.

The alternative approach was a step-wise discriminant analysis. Since the among-habitat differences in the abundance of the 15 taxa were not consistent at the four transects (Table IV-4), it was concluded that habitat comparisons should be made for each transect. Therefore, each particular habitat-transect combination defined a group and the eight groups were discriminated multivariately. A graphical representation of the results of the discriminant analysis is presented in Fig. IV-6. The discrimination of the benthic communities of the isolated pool and channel habitats at Transect D is apparent, both between themselves and also among the other six transect-habitat groups. Somewhat less dramatic is the discrimination of the isolated pool community at Transect C. Little discrimination of the two habitat types at Transect A and B is observed. Therefore, it can be concluded that the differences between the benthic communities of the channel and isolated pool habitats fall

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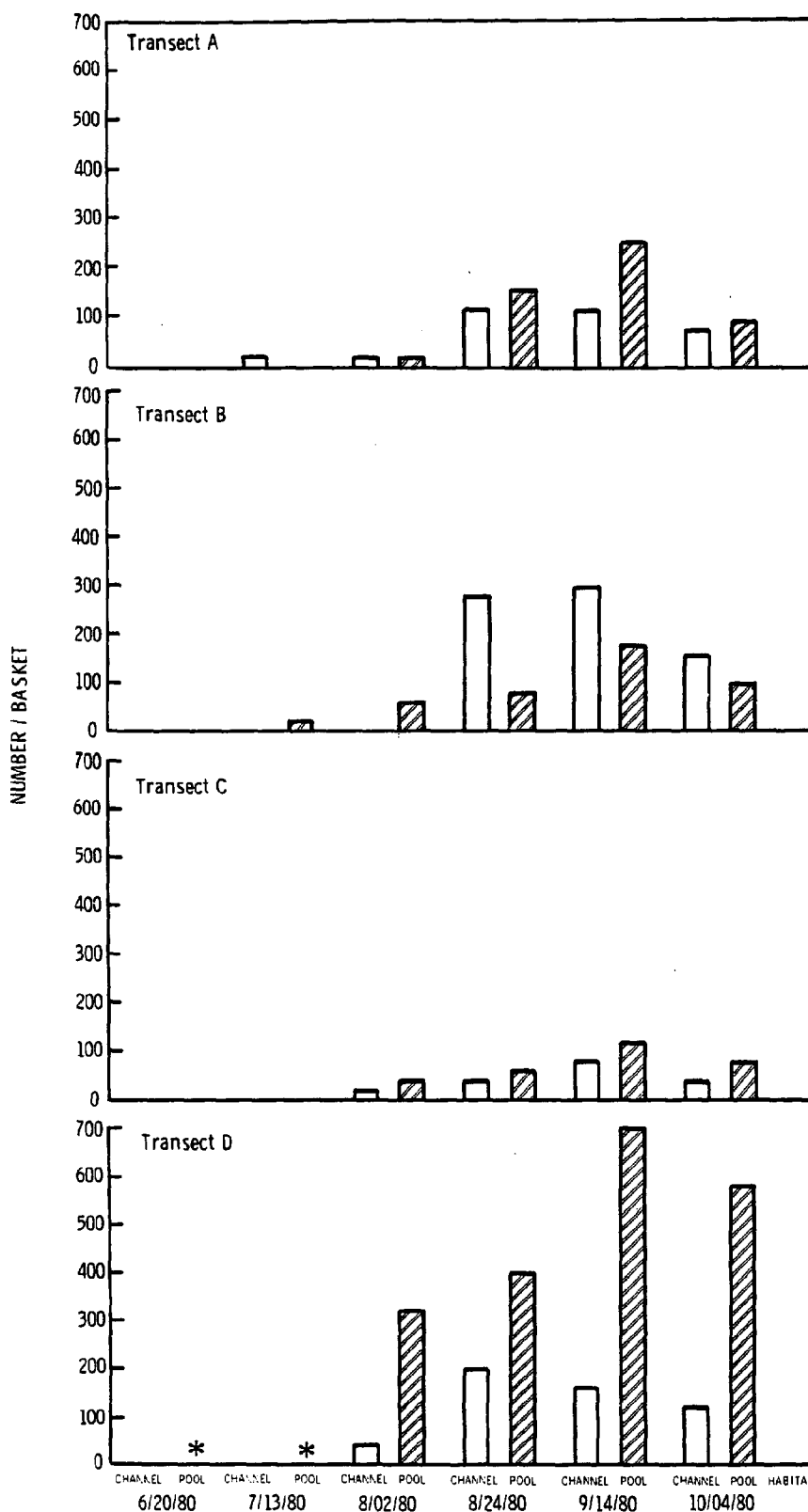


Fig. IV-3. Mean number of *Dugesia tigrina* observed in the channel and isolated habitats on each transect during the six 3- week sampling periods.
 * = No sample

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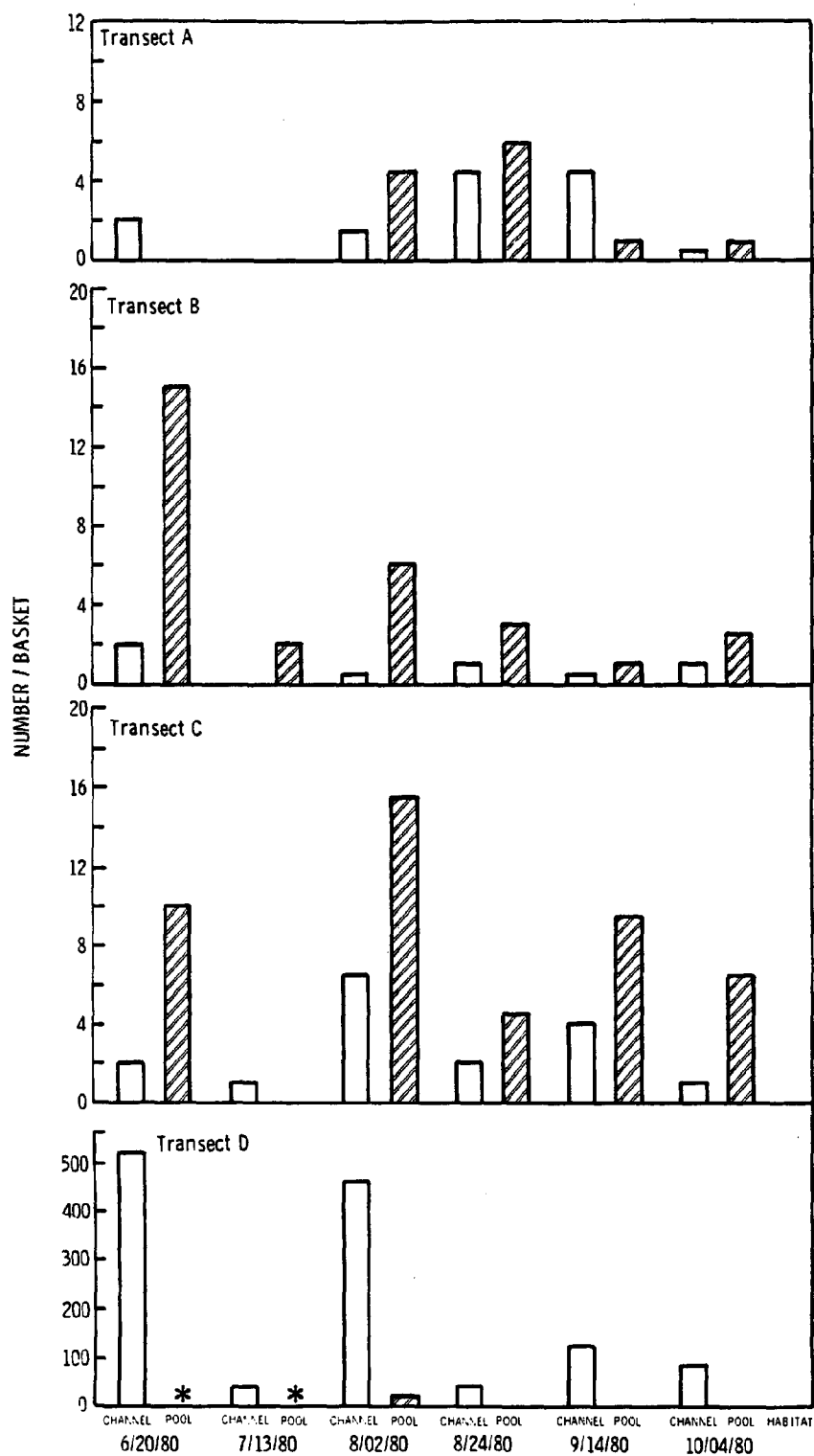


Fig. IV-4. Mean number of *Tanytarsus* spp. observed in the channel and isolated pool habitats on each transect during the six 3- week periods.
 * = No sample

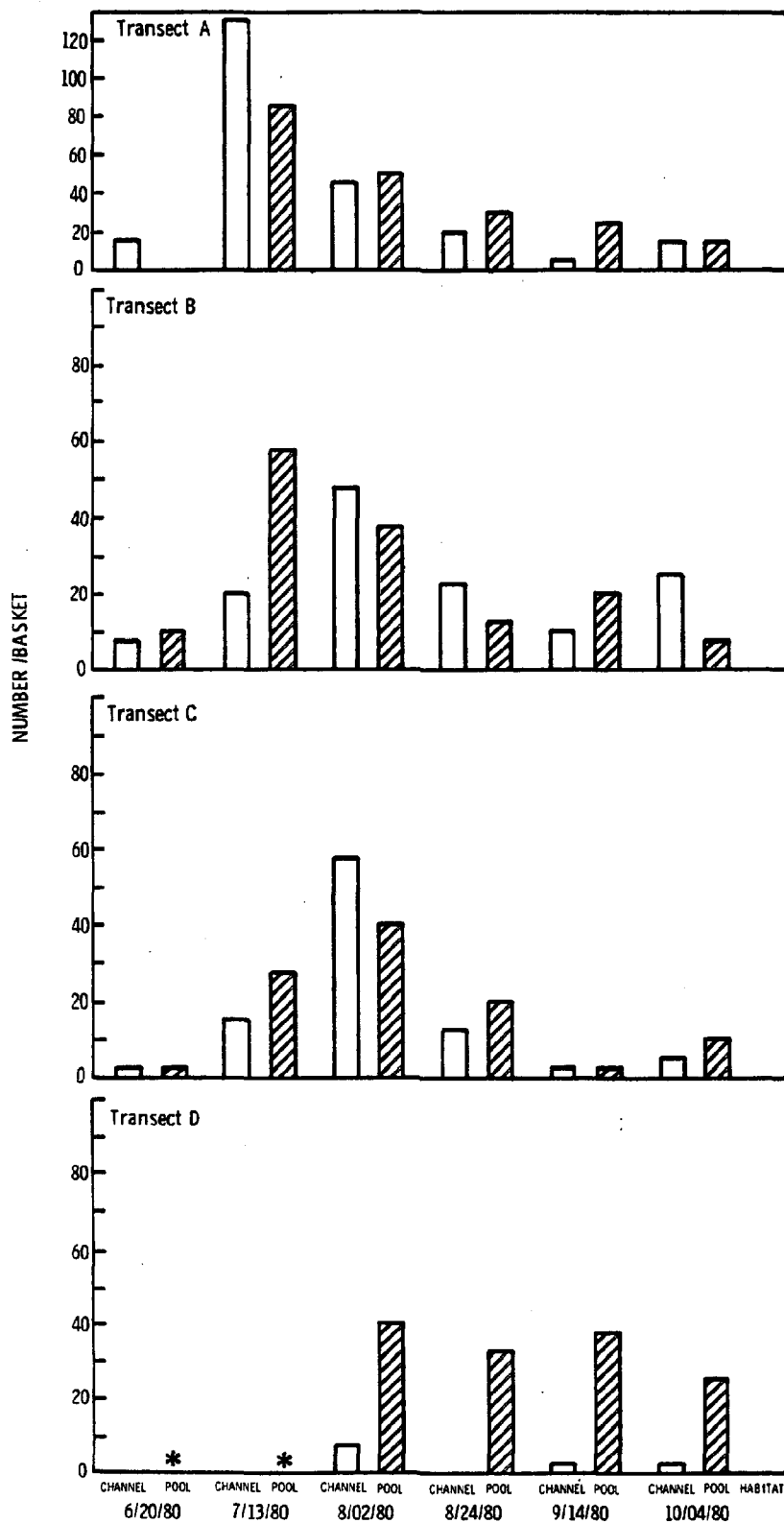


Fig. IV-5. Mean number of Gyraulis sp. observed in the channel and isolated pool habitats on each transect during the six 3- week sampling periods. * = No sample

Table IV-4. Results of three-way ANOVAs (main effects = date, transect, habitat) for 15 most abundant taxa collected in lower Susquehanna River. X indicates significance at $\alpha = 0.05$.

ANOVA EFFECTS

TAXON	DATE	TRANSECT	HABITAT	DATE x TRANSECT	DATE x HABITAT	TRANSECT x HABITAT	DATE x TRANSECT x HABITAT
<u>Gammarus lacustris</u>	X	X		X	X	X	X
<u>Dugesia tigrina</u>	X	X	X		X	X	X
<u>Dicrotendipes</u>				X			X
<u>Cheumatopsyche</u>	X	X	X		X	X	
<u>Nais pseudobtusa</u>	X	X		X	X	X	X
<u>Gyraulis sp.</u>	X	X	X	X	X	X	
<u>Tanytarsus spp.</u>	X	X			X	X	X
<u>Nais sp.</u>	X	X	X	X	X		X
<u>Hydra americana</u>	X	X		X			X
<u>Polypedilum</u>	X	X		X	X	X	X
Chironomid pupae	X			X	X	X	X
<u>Ferrissia sp.</u>	X			X		X	X
<u>Glyptotendipes</u>	X	X		X		X	X
<u>Ferrissia sp.</u>	X	X		X			

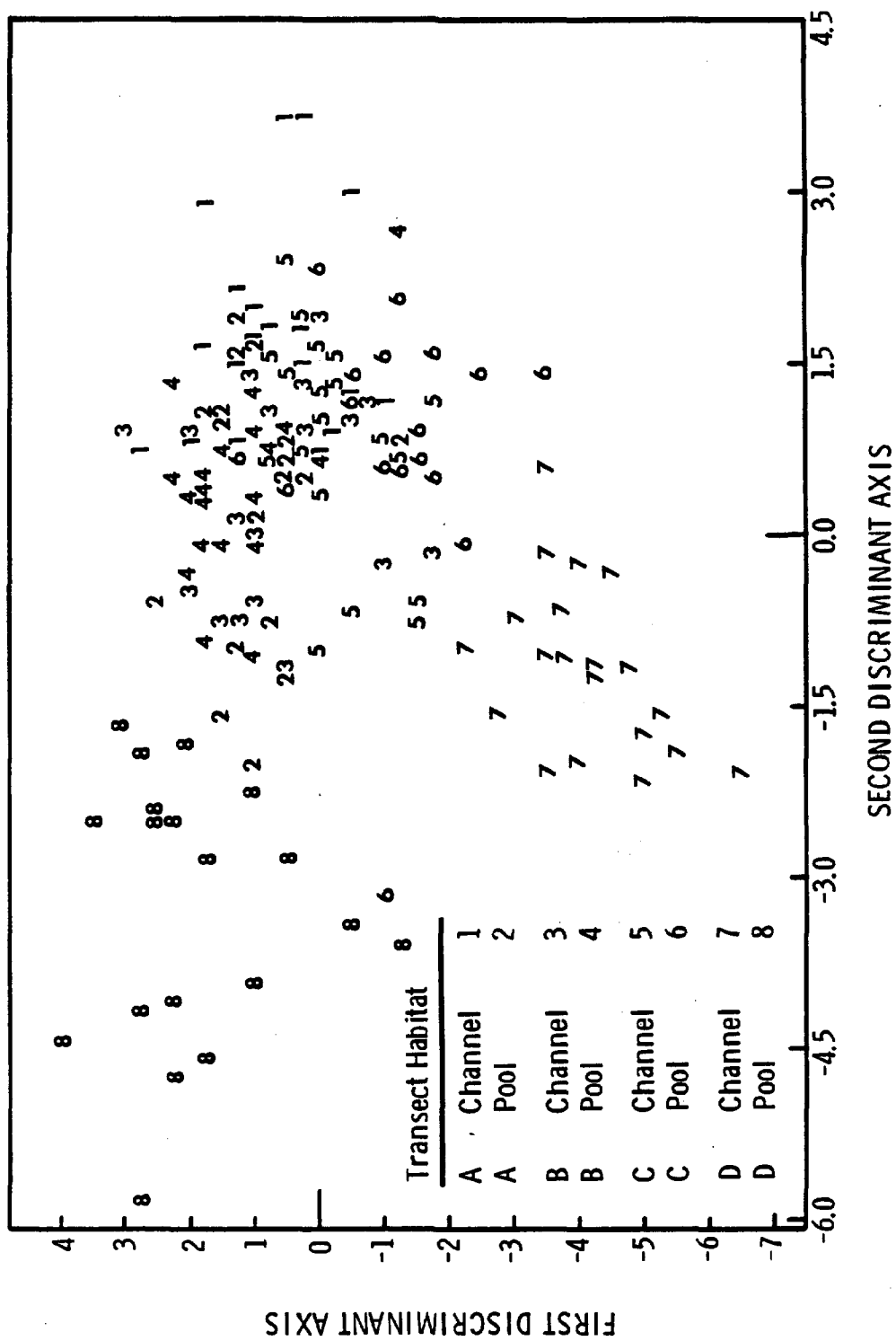


Fig. IV-6. Graphical representation of results of step-wise discriminant analysis performed on the 15 most abundant taxa taken from four transects on the lower Susquehanna River

along a gradient that ranges from large differences at the upstream river areas near the dam to small, if any, differences at the downstream transects. Pair-wise comparisons of the eight groups, made using approximate F-tests derived from Mahalanobis' D^2 (Table IV-5), show the increasing differences between the two habitat types from Transect A through Transect D, as suggested by the plot of the discriminant scores in Fig. IV-6.

Nine taxa were identified as greatest contributors to the discrimination at the eight transect-habitat combinations. Calculations of correlations between the abundances of these taxa and the linear combinations, representing the discriminant axes, identified those taxa that varied significantly along each axis. The nine taxa which best discriminate the eight groups and their correlations with the discriminant axes are given in Table IV-6. Two gastropods, Gyraulis sp. and Ferrissia sp., had significant positive correlations with the first discriminant axis. These correlations can be interpreted using Fig. IV-6. It is apparent that the separation of the points for the two habitat types from Transect D is greatest along the first discriminant axis -- the isolated pool habitat has higher discriminant scores than the channel habitats. The positive correlations for Gyraulis and Ferrissia indicate that these two taxa were relatively more abundant in the isolated pools on Transect D than in the channel habitat. Significant negative correlations with the first discriminant axis for Tanytarsus, Polypedilum, Gammarus, and Hydra indicate that their abundances were greater in the channel habitat at Transect D, not only compared to isolated pools on the same transect, but also compared to either habitat type at all other transects. Discrimination of the benthic community in isolated pools on Transect D from the other transects is greatest along the second discriminant axis (Fig. IV-6). This is due to the relatively greater abundances of Glyptotendipes and Hydra and lower abundances of Gammarus, Nais, and Dugesia in the isolated pools on Transect D (Table IV-6).

The relationships of these differences in the benthic invertebrate community to the variation in discharge from Conowingo Dam were now investigated. Table IV-7 sets out the mean discharge, fraction of time that the hydroelectric station was generating, and the frequency of changes in station operations (i.e., either from generation to no generation or vice versa) for each of the six sampling periods. These last values provide the best estimate of the number of times the areas designated as isolated pools varied from channel to isolated pool habitats. There was a continual decline in dam discharge throughout the

Table IV-5. Pairwise comparisons of eight habitat-transect groups from the lower Susquehanna River. Values presented are F values estimated from values of Mahalanobis' D^2 statistic which tests the equality of group means. Row and column headings represent transects (first letter) and habitats (second letter). * = not significant at $\alpha = 0.05$.

	AC	AP	BC	BP	CC	CP	DC
AP	3.36						
BC	1.07*	2.78					
BP	0.37*	3.0	0.86*				
CC	3.51	5.39	5.30	4.22			
CP	7.84	6.79	9.74	8.41	3.12		
DC	29.91	34.63	35.59	28.70	24.19	19.62	
DP	15.41	29.10	16.99	17.45	24.95	29.52	45.68

Table IV-6. Correlations of first two discriminant functions with the abundances of the nine taxa which most contributed to the discrimination of the eight habitat-transect groups from the lower Susquehanna River. NS = not significant at $\alpha = 0.05$.

TAXON	First Discriminant Function	Second Discriminant Function
<u>Gammarus lacustris</u>	-0.27	0.59
<u>Dugesia tigrina</u>	0.18	-0.50
<u>Tanytarsus</u> sp.	-0.89	-0.20
<u>Polypedilum</u> sp.	-0.60	NS
<u>Glyptotendipes</u> sp.	NS	-0.41
<u>Gyraulis</u> sp.	0.69	NS
<u>Nais pseudobtursa</u>	NS	-0.54
<u>Hydra americana</u>	-0.25	-0.39
<u>Dicrotendipes</u> sp.	NS	NS

Table IV-7. Mean dam discharge, fraction of each sampling period with discharge $> 63.7 \text{ m}^3/\text{s}$, and frequency of change in dam operations observed during each sampling period.

Sampling Period	Mean Discharge (m^3/s)	% of Time Discharge $> 63.7 \text{ m}^3/\text{s}$	Frequency of Changes in Dam Operations/Sampling Period
1 June - 20 June	586.1	89.3	9
20 June - 13 July	388.7	38.8	74
13 July - 2 August	300.7	43.7	87
2 August - 24 August	254.5	37.6	120
24 August - 14 September	164.5	30.7	109
14 September - 4 October	132.3	28.4	97

study period, from $586 \text{ m}^3/\text{s}$ to $132 \text{ m}^3/\text{s}$. The discharge exceeded $63.7 \text{ m}^3/\text{s}$ 89% of time during the first sampling period and was less than 45% for the remaining sampling periods. The variation of dam discharge above and below the benchmark of $63.7 \text{ m}^3/\text{s}$ was least during the first sampling period and greatest during the fourth period.

The limited number of observations (six) of the discharge parameters precluded extensive statistical evaluation of the relationship of these parameters to the observed differences in the benthic invertebrate community. However, an attempt was made to relate the results of the discriminant analysis to the discharge parameters. Mean discriminant scores along both axes were calculated for each habitat-transect combination for each sampling period. These values provide the best representation in a single number of the benthic community structure at each area during each sampling period. Differences in the scores between the two habitat types were determined for each transect and ranked. Correlations of these ranks with the ranks of the discharge parameters were then computed. No relationship between the small habitat differences on Transects A and B and the discharge parameters was found. However, at Transect C, the differences in the scores for the first discriminant function between the two habitats were negatively related ($r = 0.94$, $p < 0.05$) to mean dam discharge. That is, low dam discharge levels were coincident with the greatest observed differences in the benthic communities of the channel and isolated pools of Transect C. At Transect D, where only four observations were available due to the lack of isolated pool samples for the first two sampling periods, the differences in the mean scores for the second discrimination function were perfectly correlated with the frequency of changes in dam operations ($r = 1.0$, $p < 0.05$). Therefore, the habitat differences at Transect D increased with variation in the operation of the hydroelectric station.

V. DISCUSSION

The most obvious result of this study was the extremely low abundance of benthic invertebrates within the intermittently exposed river areas. Areas exposed for 70% of the time in summer contained only 20% of the number of individuals present in continuously submerged areas and only ca. 25% of the biomass. Similar results were obtained by Fisher and LaVoy (1972) in a study of the effect of water level fluctuations on the benthos of the Connecticut River. These authors described the intermittently exposed river areas as analogous to marine intertidal zones. In the "intertidal" river zone, however, the tidal period is irregular, the degree of exposure is seasonal (greatest in summer), and the freshwater intertidal zone is relatively new. Consequently, a stable community suited to a riverine freshwater "intertidal" has not had time to evolve (such systems have only recently appeared as the result of man-made dams). Organisms in the marine intertidal have been very successful in their adaptation to the frequency and magnitude of water-level fluctuations. However, unless some stability is established in the water levels of rivers below dams, it is unlikely that the freshwater "intertidal" zones will be inhabited by a stable, productive benthic invertebrate community.

Another notable result of the present study is the marked difference between the benthic communities found in the channel and isolated pool habitats. A number of factors may be responsible for the observed differences. The most obvious is the much lower current velocity in the isolated pool habitats below Conowingo Dam at low flow. As a result, the benthic community of the isolated pools is virtually devoid of these taxa that require flowing water to feed, i.e., filter-feeders (Merritt and Cummins, 1978). Thus, filter-feeding taxa such as Baetids, Plecopterans, and Trichopterans were present in extremely low abundances in the isolated pools; Williams and Winget (1979) and Gersich and Brusven (1981) observed similar cases. In contrast, gastropods, oligochaetes, and turbellarians were extremely abundant in the isolated pools. The most abundant gastropods, Gyraulis and Ferrissia, possess sclerotized jaws which allow them to scrape attached algae from the surfaces of rocks for food (Pennak, 1978). Rocks in the isolated pools were typically covered by a thick mat of attached algae on all four transects, thus providing a potentially

abundant food source for these organisms. Turbellarians (e.g., Dugesia) and oligochaetes (e.g., Nais) are primarily detritovores and would be well-suited to the isolated pools where detrital material is most likely to accumulate.

Channel habitats below the dam, however, contained fewer filter-feeding taxa than might be expected. Only Hydra, a filter-feeder which collects drifting plankton, was present in appreciable numbers within the channel habitats, and then only at Transect D. This finding is not surprising since its food source (plankton discharged from the reservoir), would be most abundant at this most upstream transect. The other taxa which were most abundant in the channel habitats, especially at Transect D, were Gammarus, Tanytarsus, and Polypedilum. These types feed by shredding coarse particulate organic matter, which may be more continuously abundant in this area due to the withdrawal of seston-rich waters from the hypolimnion of Conowingo Pond. A downstream decrease in abundance of these organisms may have been related to the decreased velocities at Transects A and B at the low discharge levels, compared to those at the upstream transects. The bottom geometry of the river bed is the probable cause of these differences in current velocity since the channel at Transects A and B is much wider than at the upstream transects.

Another factor that may be an important determinant of benthic invertebrate community structure in the two habitats is dissolved oxygen (DO) concentration. Since the water released from the reservoir is hypolimnetic, its DO concentration from mid- to late-summer is often extremely low. Thus, large fluctuations in DO below the reservoir are common as a result of the irregularity in dam discharge. Benthic invertebrates below the dam are thereby subjected to periods of stress, which may exclude taxa that are intolerant of low DO conditions. Although organisms in both the channel and isolated pool habitats are exposed to these periods of stress, diel variation in DO concentrations in the isolated pools can be extreme, ranging from supersaturation near mid-day to levels near anoxia at night (ERM, 1981). These fluctuations are most common over weekend shutdown periods, when little, if any, water enters or leaves the isolated pools. The taxa inhabiting these areas must necessarily be more tolerant to fluctuations in DO concentrations than those in the channel habitats. The study findings support this hypothesis: the gastropods, oligochaetes, and turbellarians found in the isolated pools are characteristically present in other environments where low DO concentrations are prevalent (Pennak, 1978).

The differences in the benthic invertebrate communities at the three habitat types in the lower Susquehanna River may be very important for the resident finfish communities. It is quite apparent that the total amount of available food for resident fishes is reduced when large portions of the river bed are exposed, i.e., during the periods when the turbines are not operating. The differences in the structure of the benthic communities in the channel and isolated pools may also have a profound effect on the ability of fish to gather food in this portion of the river. Detailed studies of the feeding habitats of the important fishes in this region would provide valuable information on whether such organisms as gastropods, present in extremely large numbers in isolated pools, are being fed upon. Answers to such questions are necessary for informed judgments of the effect of possible alternative turbine operating procedures on the fishes of the Susquehanna River below Conowingo Dam.

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